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BOOK REVIEW

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# Book Review: On ecological networks and biological invasions

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**Invading Ecological Networks by Cang Hui and David M. Richardson, Cambridge University Press, 2022. 423 pp. hbk.: US$115.00, ISBN 9781108478618; pbk.: US$ 49.99, ISBN 9781108745963**

There are several remarkably active research areas in contemporary ecology. Biological invasions and study of ecological networks are two of them. Since the SCOPE international programs, initiated in the final decades of the last century, the number of publications on biological invasions has been increasing exponentially. Besides NeoBiota, at least five other current journals are completely dedicated to this topic. The number of publications on ecological networks has been also increasing and recent years have seen a burst in the study of this subject (e.g., Polis and Winemiller 1996; Pascual and Dunnde 2006; Dáttilo and Rico-Gray 2018; Losapio et al. 2019; Guimaraes 2020; Kéfi 2020; Benadi et al. 2022). Twenty-three volumes of the journal “Food Webs” have been published since 2014. More than 1300 ecological networks are included in Mangal – a database for species interaction networks (Poisot et al. 2021). Therefore, combining these two areas into one treatment was a good idea. True, the attempt by Hui and Richardson is not the first one (e.g., Romanuk et al. 2009; Galiana et al. 2014; Lurgi et al. 2014; Kinlock and Munch 2021). Nevertheless, building on their previous journal articles, mathematician Cang Hui and plant ecologist David Richardson provide, in 423 pages, the most ambitious attempt to synthesize the two research areas so far.

The book is divided into seven chapters. The first chapter summarizes what authors call invader-centric “Invasion Science 1.0” and sets a stage for a more complex new world of “Invasion Science 2.0” that is developed in the following chapters. The sum-

mary provided in the first chapter, while sketchy, is mostly accurate. The authors' multiple complaints about context dependence and low predictability of existing invasion hypotheses is certainly justified. One important aspect that has been for some time already part of "1.0" and is omitted from this summary is the accent on phylogenetic relatedness in many recent studies of biological invasions (e,g., Strauss et al. 2006; Diez et al. 2008; Cadotte et al. 2009; Schaefer et al. 2011; Cadotte and Davies 2016; Park et al. 2020; Schmidt et al. 2021). This research is, however, touched at the end of the second chapter.

It is not completely clear to whom the book ("a hitchhiker's guide" as it is characterized by the authors) is addressed. However, if biologists are among them, they may be, unfortunately, discouraged by the very first equation in this chapter. The equation (1.1) describes spreading dynamics of biological populations: $\partial n/\partial t = rn(1 - n) + D(\partial^2 n/\partial x^2)$. We learn in the text that $n$ represents the population density and is a function of time $t$ and location $x$; the left of this equation describes the time derivative of population density; the first term on the right depicts a simple logistic growth, with the intrinsic rate of growth $r$. In ecological literature, population density is usually measured in terms of number of individuals, and a biologically trained ecologist will therefore probably be puzzled by the expression $rn(1 - n)$ ("a simple logistic growth" according to the authors) predicting that in equilibrium (when the density of logistically growing population reaches what is called "carrying capacity"), the population would consist of only one individual ($n = 1 \Rightarrow 1 - n = 0$). Therefore, unless $n$ means something else than number of individuals, using $rn(1 - n/K)$ where $K$ is a scaling constant, i.e. carrying capacity (Murray 2004, p. 400; Cosner 2012, p. 607), instead $rn(1 - n)$, would be preferable. Nevertheless, readers should not be deterred by this confusion. The book provides a large collection of potentially applicable mathematical procedures for dealing with multispecies systems, mainly for theoretical ecologists, as well as references to many empirical studies that may be interesting for biologists.

The second chapter ("Relentless Evolution") is dedicated to species interactions, their coexistence, and co-evolution of traits. Here we learn about some conceptually useful approaches to quantification of interaction strength in the realm of Hessian interaction matrices. After that, we explore different kinds of equilibria and the Lyapunov stability of such systems. In this context, conditions for invasion and coexistence can be determined as inequalities in values of particular parameters (including competition coefficients and carrying capacities), their ratios, fitness differences, and niche separations. A call for studies of the impacts of higher-order interactions is certainly justified. Some basic concepts of evolutionary biology are recalled here and the importance of adaptive interaction switching is inevitably stressed because it is important in the context of dynamic ecological networks. Interaction strength is then expressed as a niche-based interaction kernel that is a function of the relevant traits of interacting species. Because co-evolution of traits could explain structures of many ecological networks, the rest of the chapter is dedicated to this topic. This is done mostly via references to rather demanding theoretical concepts (canonical equation of adaptive dynamics, convergence stable singularity, evolutionary stable strategy, continuously

stable strategy, Price equation, etc.). The evolution of competitive ability of invasive species (EICA) is mentioned in this context.

Chapter 3 ("Network Assembly") is the core of the presented network-invasion synergy. It explores how structures of ecological networks emerge from interactions among species. First, a history of ideas about mechanisms of ecological succession and community assembly processes is extensively reviewed. Almost all relevant concepts and ongoing debates in contemporary ecology are packed into the introduction to this chapter. To summarize current knowledge, the authors proposed sorting non-random patterns in invaded biotic communities along three types of dispersion: temporal, spatial, and ecological. The first one is reflected in time series of abundance, species richness or other relevant variables that may or may not reflect shifts due to invasions or some other environmental changes. Such changes may be associated with dynamics and instability of invaded ecological networks – the topic covered in chapters 4 and 5. Spatial dispersion amounts of spatial patterns of species under interest – their positive or negative associations and aggregations. In this context alpha, beta and zeta (developed by Hui and McGeoch 2014) indices of diversity are introduced. Ecological dispersion is a measure of the functional similarity or dissimilarity between resident species. Basic concepts of network topology and architecture are introduced (connectance, linkage density, node degree, centrality, modularity, nestedness, etc.). Then, three types of networks are distinguished: competitive, antagonistic and mutualistic.

The results of several recent studies of plant communities and food webs are reviewed. A multivariate plant community analysis of *Clidemia hirta* invasion in Sabah (Fig. 3.14) is a nice example. Decline of connectance with network size (for the first time documented by Rejmánek and Starý 1979) is discussed and some results showing increase of invasion resistance with increasing connectance are presented. However, whether there is a general causal connection remains an open question. The enemy release hypothesis, as well as the evolution of increased competitive ability is mentioned here again. Whether there is some fundamental difference in the structure of antagonistic and mutualistic networks remains to be properly analyzed with respect to network-area relationships. Examples of invasions into mutualistic networks are listed and a conceptual framework for inferring establishment success and invasion performance of introduced legumes is provided (Fig. 3.20). Several examples illustrate changes in network structure due to invasions (e.g., an increase of nestedness in pollination networks). Inevitably, a special research challenge is posed by ecological networks with multiple (trophic and non-trophic) interaction types. The rest of the chapter is dedicated to the role of co-evolution in the emergence of dynamic and adaptive networks. Several original contributions of Cang Hui are utilized in this context. Finally, Daniel Janzen's concept of ecological fitting (the formation of biotic interactions without co-evolution) is utilized to explain the novel interactions between species that had shared little evolutionary history. A list of more than 300 references concludes this chapter.

Chapter 4 ("Regimes and Panarchy") explores how invasion performance and invasibility are related to the loss of network stability or instability. To do that, the authors first define a complex adaptive system (CAS) as "a dynamic system comprising

multiple interacting parts that respond, adaptively and collectively, to perturbations, often reactively but sometimes actively or proactively." Then, several different concepts and definitions of stability applicable on a CAS are presented. Inevitably, such a topic has to start with Robert May's stability criterion and its extensions. (There is an incorrect reference to May 1973; it should be a reference to his book, not the article in The American Naturalist.) As the authors correctly reproduce, stability of May's random community matrices decreases with their complexity. However, stability of matrices representing competition communities may increase with connectance (Rejmánek et al. 1983; Rozdilsky and Stone 2001; Fowler 2009). From a theoretical point of view, this is an extremely interesting research area. However, sooner or later we have to realize that there are serious problems with the application of stability criteria based on eigenvalue analyses of real systems defined by their size, connectance, nestedness and interaction strengths. Reliable estimates of these parameters are obtained only very rarely from real laboratory or natural biotic communities (Seifert and Seifert 1976; Roxburgh and Wilson 2000; Fox and McGrady-Steed 2002; Carrara et al. 2015).

Nevertheless, the discussion about how these parameters may be changed via propagule pressure, niche occupation, fluctuating resources, etc. (p. 224) may lead to some new research directions. Also, some theoretical studies are supported by empirical data. For example, modeling studies show that a highly connected and nested architecture promotes stability in mutualistic networks, while the stability of trophic networks is enhanced in compartmented and weakly connected communities. A meta-analysis of the architecture of 57 real networks supports this prediction (Thébault and Fontaine 2010).

The rest of the chapter is dedicated to the formal descriptions and examples of regime changes, adaptive cycles (panarchy), collapses and meltdowns in invaded networks. To illustrate a possibility of the construction of interaction matrices, the authors used available data on the well-studied biocontrol agent, ladybird *Harmonia axylaris* that is predicted to be a major threat to other species within the aphidophaguous guild. Based on the literature and expert opinions, the authors compiled the semi-quantitative interaction matrices of agricultural and forest systems that are currently invaded by this species (Fig. 4.15 and Hui et al. 2016). Based on the eigenvalue analysis, both systems are asymptotically stable before the invasion. After invasion, both systems become ecologically unstable, with the forest more than the agricultural system, suggesting stronger impact of the invader on the forest from the perspective of the aphidophagous guild stability. This is a nice example of how even rather tentative data can be used to make interesting inferences.

Finally, the potentially useful concept of marginal instability (self-organized criticality, Solé et al. 1999) is introduced in this chapter. Driven by constant input of propagules and successful invasions, open adaptive networks operate close to instability. Because of that, the stability-complexity relations discussed earlier in this chapter are either weak or lacking in such networks. Surfing in gentle waves is used as a metaphor illustrating systems under persistent transition at marginal instability (criticality).

Chapter 5 ("Network Transitions") explores the dynamics of ecological networks resulting from invasion-induced instabilities. Of course, this is a domain where pre-

dictability is very low and forecasting inherently unreliable. However, to outline some options, the authors introduce (1) "early warning signals" of bifurcation/regime shifts in ecological systems (inevitably, such signals are highly system specific); (2) "temporal turnover" of residing species and network interactions (theory of island biogeography is a starting point for actual monitoring and generalizations); (3) "weather vane" as an indicator of the transient dynamics of network turnover (such short-term indicators would certainly be helpful if required Hessian and Jacobian matrices were available). Finally, the role of rare species in maintaining system stability, functionality and invasibility is discussed. Conclusion: ". . . rare species hold the key to network instability and invasibility, while the commonness-rarity gradient, captured by the weather vane, gives us the direction and magnitude of temporal turnover."

Chapter 6 ("Network Scaling") deals with the fact that ecological networks are not isolated, but embedded in larger systems (meta-webs, meta-communities). Assembly of any open ecological networks depends on constant influx of alien or regionally native species and extinction of species that were present earlier. Therefore, fitting a particular network into a broader landscape context is one topic covered in this chapter. Another topic is spatial scaling. The structure and functioning of ecological networks change with spatial scales at which they are analyzed. As the authors correctly point out, such scale dependence creates both problems and opportunities for our understanding of real nature. Several relevant questions, including scale dependent correlation of native and exotic species are discussed here. Meta-network dynamics, stability criteria of meta-networks and the role of dispersal in meta-network transitions are covered in the rest of the chapter. This is an area of active research and some new, mostly theoretical, results emerged since the book was written (e.g., Erös et al. 2020; Clark et al. 2021; Galiana et al. 2022; Liu et al. 2022; Saravia et al. 2022; Yang and Bao 2022). I would expect that more attention will be paid to quantification of environmental spatial heterogeneity and its effects on the pattern and processes discussed in this chapter.

The final chapter ("Rethinking Invasibility") attempts to provide a fresh look at the classic problem of invasion biology: how trait-mediated interactions can cause invasions and impacts in the recipient biotic communities. First, the major points in the previous chapters are reiterated. Then, apparently as a backbone of the "Invasion Science 2.0", a model of the eco-evolutionary dynamics of an open adaptive network (Hui et al. 2021) is presented. Conceptually and mathematically, this is a beautiful model. It certainly stimulates nontraditional and multidimensional thinking about biological invasions. Eventual parametrization of the four equations in this section is left to the readers. Nevertheless, some intuitively expected generalizations emerge from this model: ". . . to be successful, invaders need to position their traits relative to the trait distributions of resident species from different functional guilds. They must also mitigate negative interactions by occupying peripheral trait positions and increase positive interactions by seeking central trait positions." Perhaps some generalizations based on field and laboratory studies of invasions (e.g., Kimball et al. 2013; Fridley et al. 2022) will find their place within this framework. It seems that at the end of this final chapter, the authors felt an obligation to say something about management. This resulted in

many correct but rather trivial statements with only a very loose connection to the rest of the book. There are several management related topics that are not covered, but will be important in the near future. For example, with ongoing climate change, maintenance of demographic/taxonomic composition will be less important than the functional stability – persistence of biomass production, carbon sequestration and climate regulation (e.g., Loreau et al 2001; Mathes et al. 2021). Also, interactive effects of invasions, habitat loss and global warming are a highly timely research area. The extensive Glossary (14 pages) after the last chapter, will be very helpful for all readers.

At the end of the preface, the readers are warned: "It is not a recipe book. . .". Still, many ecologists would be interested to learn more of a real world where the data on ecological networks could be collected and analyzed. For example, problems with different kinds of sampling bias (Costa et al 2016; Fründ et al. 2016; Brimacombe et al. 2022) and taxon resolution (Hemprich-Bennett et al. 2021), are not trivial. Obviously, there is an open niche for a different book showing how to do it in the field. Of course, this does not diminish the value of the book under review. It will provide a lot of inspiration for theoretical ecologists and mathematicians. Biologists, if they are not discouraged by mathematical concepts and expressions, will find many interesting references and ideas. Very likely, they will conclude that what is presented here is not really completely new to them. The novelty stressed by the authors is not really so new. Ecologists working on biological invasions are well aware of the multispecies and multidimensional complexity of their subject. Therefore, there is no need to break through an open door.

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